

FEEDING OF *NEOMYSIS MERCEDIS* (HOLMES)¹

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The opossum shrimp, *Neomysis mercedis*, is found in brackish to fresh water from Alaska to California, where it is an important component of estuarine food webs. In the San Francisco Bay Delta, it has been shown to be an important food organism for young striped bass (Heubach *et al.*, 1963; Stevens, 1966a), American shad (Stevens, 1966b), white sturgeon (Radtko, 1966), white catfish (Turner, 1966), and the caridean shrimp of the Delta (Siegfried *et al.*, 1978).

Mysids are generally regarded as omnivorous, feeding on detritus, algae, and zooplankton (Bowers and Grossnickle, 1978; Kost and Knight, 1975; Mauchline, 1971; Tattersall and Tattersall, 1951) by virtue of their ability to feed raptorially as well by filtering (Tattersall and Tattersall, 1951). The relative role of each feeding method has received limited attention. Lasenby and Langford (1973) suggested that *Mysis relicta* changes from a benthic detritivore-herbivore during the day to an active predator at night. Richards *et al.*, (1975) postulate that *M. relicta* has been responsible for the decline of large zooplankters in Lake Tahoe, California. Additional studies suggest that copepod predation may be the most important source of food for *M. relicta* in Lake Tahoe (Rybock, 1978; Morgan, 1979). Previous studies of *N. mercedis* have characterized it as omnivorous but made no attempt to determine the relative importance of the various food materials to the total energy intake of the mysid populations (Kost and Knight, 1975; Wilson, 1951).

The only information available indicates that detritus and diatoms are the most abundant items in the gut of *N. mercedis* from the Sacramento-San Joaquin Delta (Kost and Knight, 1975). Crustacean fragments, rotifers, and tintinnids were also found in the gut, but their contribution to the mysids' diet was not examined. Studies of other mysids suggest that they take whatever food is available in their immediate environment (Mauchline, 1967, 1971; Raymont *et al.*, 1964). A recent study of herbivorous feeding by *M. relicta* in Lake Michigan demonstrated algal selection based on size (Bowers and Grossnickle, 1978). Information is lacking on prey selection by *N. mercedis*.

Mysids cultured in the laboratory feed readily on crustaceans such as *Artemia salina* and barnacle nauplii (Foulds and Mann, 1978; Mauchline, 1971). We have held specimens of *N. mercedis* in our laboratories with *Artemia* nauplii as the only food source. Since *N. mercedis* can be an efficient predator in the laboratory, it may also be an important predator in the estuary. This paper evaluates prey selection (both phytoplankton and zooplankton) and the role of carnivory in the nutrition of *N. mercedis* in the Sacramento-San Joaquin Delta.

MATERIALS AND METHODS

The study was conducted as part of a broad baseline investigation of the aquatic resources of the Sacramento River-Suisun Bay portion of the San Francisco Bay-

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Delta Estuary (Seigfried *et al.*, 1978). Sample specimens of *N. mercedis* were collected for gut analysis from two sites at roughly bimonthly intervals from January through November, 1976. One station was located at Chipps Island in eastern Suisun Bay (Station M7), and the other in the Sacramento River channel of the Bay-Delta, about 2 km west of Decker Island (Station M1).

Mysids used for gut-content analysis were selected from samples collected in tows with a #8 plankton net (mesh = 20 μ m) and preserved in 5% buffered formalin. Selected for gut-content analysis were specimens of *N. mercedis* of three different sizes: mature mysids 10–11 mm long, immature mysids 7 mm long, and juvenile mysids ≤ 3 mm long (January–August; few found in September–November). Slides were prepared by removing the guts of 8 mature mysids, 10 immature mysids, or 20–25 juvenile mysids; teasing them open, and filtering the pooled contents onto 0.45- μ m Millipore filter pads. The entire filter pad was examined at 40 \times for crustacean or rotifer remains, which were quantified by searching for rami, antennae, or loricas. All phytoplankton prey present on the filter pads were counted and identified from January through August, and perpendicular strips of each filter pad were counted in September and November. The relative amount of each food item was determined by examining 10 microscope fields at 200 \times and estimating the portion of the field occupied by each item. A Whipple ocular micrometer was used to divide the fields into smaller units for approximating percent coverage.

Prey availability was determined from phytoplankton and zooplankton samples collected at the time of the mysid collections. Phytoplankton samples were obtained from depths of 1, 2, 5, 7, and 9 m and preserved in Lugol solution. Four replicate counts of each phytoplankton sample, with identifications to the generic level, were conducted by the Utermöhl inverted-microscope technique (640 \times) (Schworbel, 1970). A Whipple ocular micrometer was used to determine cell dimensions. Three replicate zooplankton samples were collected at the same depths as above by a diaphragm-pump method (Herrgesell, 1975) using a #20 plankton net (mesh = 80 μ m). Counts were made of the entire sample at 45 \times in all months except March, when it became necessary to sub-sample for rotifers. A mean for the entire water column was used to estimate prey availability.

Laboratory feeding experiments used *N. mercedis* and *Eurytemora hirundoides* collected in the Delta and held in laboratory culture tanks. Experiments were conducted at 17°C in sea water reconstituted to obtain test water with a salinity of 4‰. Four to 32 individuals of *E. hirundoides* were added to 300 ml of water in each of eight 500-ml flasks. Four flasks were taped to exclude light, and four were clear. One mature unstarved mysid was added to each flask except for one light and one dark "control" flask. Feeding experiments were terminated after 12 hr and the number of copepods remaining in each flask determined. If copepod mortality was significant in the control flask, the results were discarded.

RESULTS

The phytoplankton of the San Francisco Bay Estuary is diverse, with more than 120 species identified (California Department of Water Resources, unpublished). More than sixty genera, primarily diatoms and green algae, were identified in the present study, and more than half of those have been identified in the gut contents of *N. mercedis* (Table I).

TABLE I

Phytoplankton genera identified from samples collected in the Sacramento-San Joaquin Delta Estuary, January–November, 1976. Genera identified in *N. mercedis* guts are indicated by +.

CHIRY SOPHYTA	+ <i>Melosira</i>	<i>Crucigenia</i>
+ <i>Achnanthes</i>	+ <i>Meridion</i>	<i>Golenkiniopsis</i>
<i>Amphipleura</i>	+ <i>Navicula</i>	<i>Gonium</i>
<i>Amphiprora</i>	+ <i>Nitzschia</i>	<i>Microspora</i>
+ <i>Amphora</i>	+ <i>Pinnularia</i>	<i>Oocystis</i>
+ <i>Asterionella</i>	+ <i>Pleurosigma</i>	+ <i>Pediastrum</i>
<i>Bacillaria</i>	+ <i>Rhoicosphenia</i>	<i>Pleurotaenium</i>
<i>Caloneis</i>	+ <i>Rhopalodia</i>	<i>Radiofilum</i>
<i>Chaetoceros</i>	+ <i>Skeletonema</i>	<i>Scenedesmus</i>
+ <i>Cocconeis</i>	+ <i>Stauroneis</i>	<i>Selenastrum</i>
+ <i>Coscinodiscus</i>	+ <i>Stephanodiscus</i>	<i>Staurastrum</i>
+ <i>Cyclotella</i>	+ <i>Surirella</i>	<i>Ulothrix</i>
+ <i>Cymatopleura</i>	+ <i>Synedra</i>	
+ <i>Cymbella</i>	+ <i>Tabellaria</i>	DINOFLAGELLATES
+ <i>Diatoma</i>	<i>Tropidoneis</i>	(PYRRHOPHYTA)
+ <i>Diploneis</i>		<i>Glenodinium</i>
+ <i>Epithemia</i>	GREEN ALGAE	+ <i>Peridinium</i>
+ <i>Eunotia</i>	(CHLOROPHYTA)	
+ <i>Fragilaria</i>	<i>Actinastrum</i>	BLUE-GREEN ALGAE
+ <i>Frustulia</i>	<i>Ankistrodesmus</i>	(CYANOPHYTA)
+ <i>Gomphonema</i>	<i>Chaetophora</i>	<i>Anabaena</i>
+ <i>Gyrosigma</i>	<i>Chodatella</i>	<i>Merismopedia</i>
<i>Hantzschia</i>	<i>Closteriopsis</i>	<i>Nodularia</i>
<i>Mallomonas</i>	<i>Closterium</i>	<i>Oscillatoria</i>

The composition of the phytoplankton community changed seasonally during 1976. Various centric diatoms dominated the plankton flora from January through September, and a small blue-green alga, tentatively identified as *Mersmopedia* sp., was dominant in November (Fig. 1), although diatoms continued to dominate the biomass. Phytoplankton density peaked in the spring of 1976 and was lowest in August (Fig. 2). The pattern of phytoplankton population density and composition was similar at both stations.

Zooplankton dynamics within the study area in 1976 were influenced in part by low delta outflows. In January, salinities were low, and the associated fresh-water group of organisms—*Cyclops*, rotifers, and cladocerans—dominated the upstream area (Fig. 3). Rotifers, primarily *Keratella* and *Notholca*, dominated in March. During the remainder of 1976, the fresh-water association was gradually replaced by a brackish-water group dominated by *Eurytemora hirundoides*. By November, a higher-salinity association dominated by *Acartia clausii* and specimens of *Synchaeta* appeared in the study area. Densities reached a maximum in March, coincident with the spring diatom increase. Zooplankton densities were lowest in January. Table II lists the zooplankton collected in the study area in 1976.

Although diatoms were numerically the most abundant prey in the mysid guts, unidentifiable amorphous material and animal fragments generally covered the greatest portion of the filter pads (Fig. 4). Composition of the diet varied in relation to mysid size and location in the estuary. Diatoms composed the greatest percentage of the diet at the upstream site in May. Diatoms accounted for > 50%

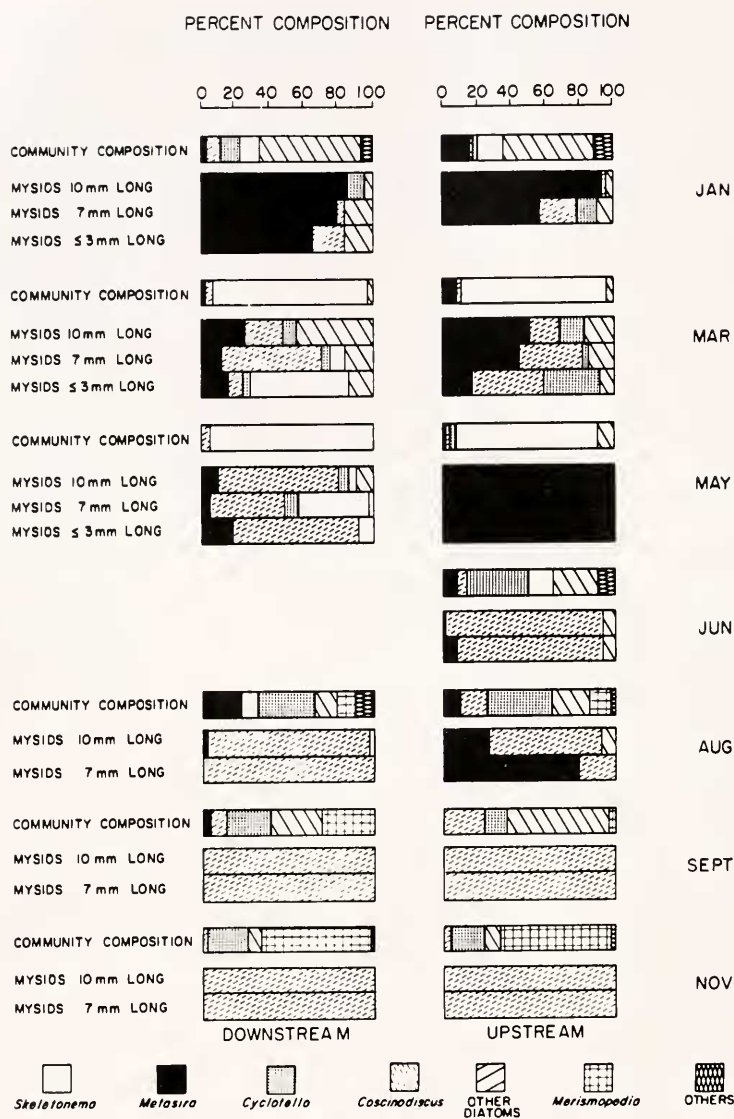


FIGURE 1. Composition of phytoplankton community and phytoplankton consumed by *N. mercedis* in Sacramento-San Joaquin Delta Estuary, January–November, 1976.

of the gut materials on one occasion only, at the upstream site in May. The contribution of diatoms to the diet generally decreased with increasing mysid size.

Crustacean fragments were not found in the guts of mysids ≤ 3 mm long, but rotifers were present in these guts in May (Figs. 3, 4). Animal remains were relatively abundant in the guts of mysids of the larger size classes.

Selective feeding is evident in every month and in all sizes of mysids (Figs. 1, 3). A strong positive selectivity for *Melosira* was evident among all sizes of

mysids from January through May. In March and May, although *Skeletonema* was very abundant, accounting for > 90% of the phytoplankton present, it accounted for only a small portion of the diet. From June through November, except for the upstream station in August, *Coscinodiscus* dominated the mysid diet, while all other forms were "negatively selected."

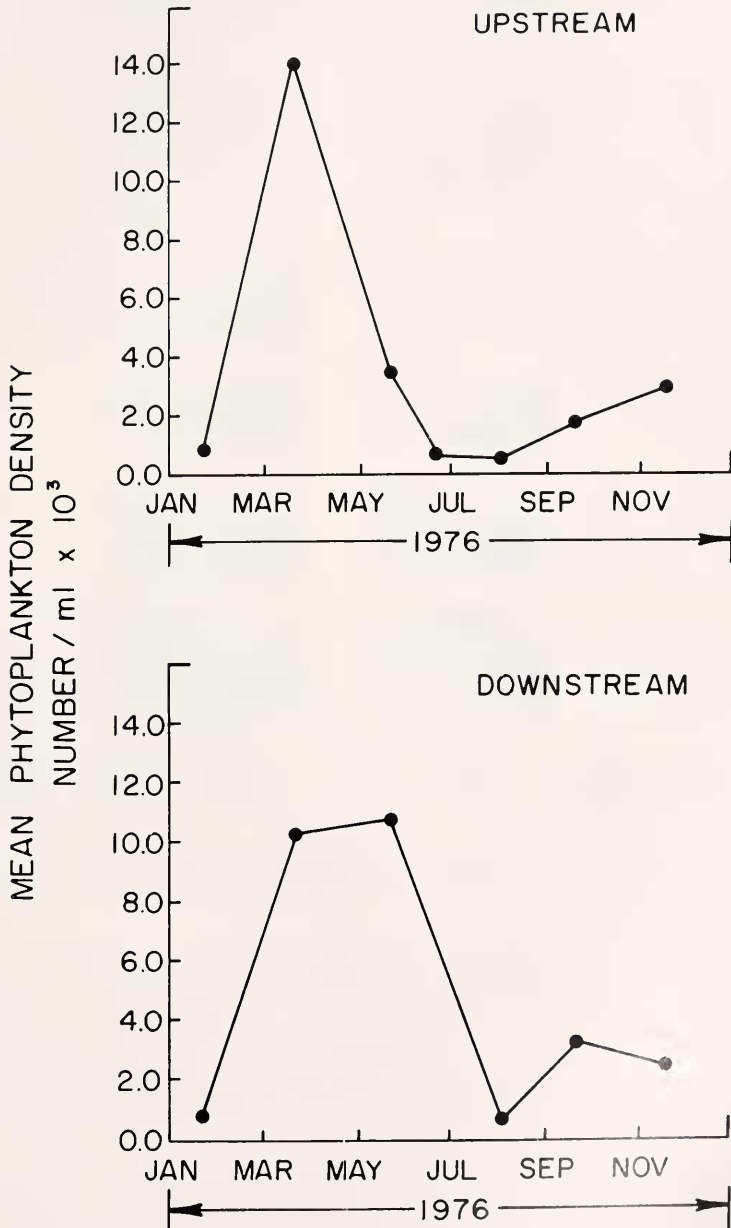


FIGURE 2. Mean density of phytoplankton at upstream (Station M1) and downstream (Station M7) sites in the Sacramento-San Joaquin Delta Estuary, January–November, 1976.

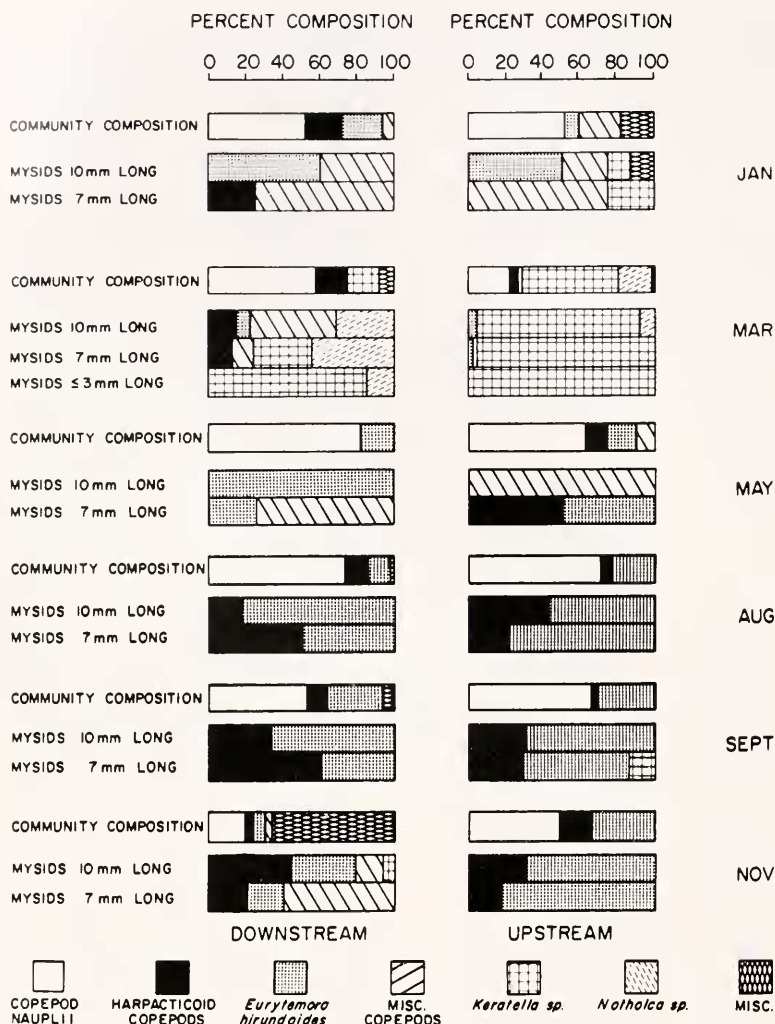


FIGURE 3. Composition of zooplankton community and zooplankton consumed by *N. mercedis* in Sacramento-San Joaquin Delta Estuary, January–November, 1976.

Selection was also evident among mysids feeding on zooplankton. Although copepod nauplii were generally the most abundant crustacean plankters in the system, none were evident in the gut contents of *N. mercedis* (Fig. 3). Rotifers were abundant in March and preyed upon heavily by *N. mercedis*, averaging 29/mysid at the upstream station. *Keratella* and *Notholca* were the rotifers ingested most frequently although additional soft-bodied forms, i.e., *Synchaeta*, may have been ingested but not recognized in the gut contents.

Eurytemora hirundoides and harpacticoid copepods (adult and copepodites) were the crustaceans (Fig. 3) eaten most frequently. Mysids ≥ 7 mm long caught each month except November and March had consumed an average of one to two copepods each. In November and March, the average was three to four copepods in each gut. The largest mysids (≥ 11 mm) always consumed more

TABLE II

Fauna collected in zooplankton samples from the Sacramento-San Joaquin Estuary, January–November, 1976.

COPEPODS	ROTIFERA
<i>Eurytemora hirundoides</i>	<i>Polyarthra</i> sp.
<i>Acartia clausii</i>	<i>Kellicottia</i> sp.
<i>Diaptomus</i> sp.	<i>Filinia</i> sp.
<i>Cyclops</i> sp.	<i>Synchaeta</i> sp.
<i>Ectinosoma</i> sp.	<i>Keratella</i> sp.
<i>Scottalana</i> sp.	<i>Notholca</i> sp.
undet. Harpacticoid a	<i>Brachionus</i> sp.
undet. Harpacticoid b	<i>Platyias</i> sp.
CLADOCERA	<i>Asplanchna</i> sp.
<i>Bosmina longirostris</i>	<i>Ascomorpha</i> sp.
<i>Daphnia laevis</i>	<i>Tetrasiphon</i> sp.
<i>D. pulex</i>	<i>Pleurotrocha</i> sp.
<i>D. schodleri</i>	<i>Trichotria</i> sp.
<i>D. galeata</i>	<i>Wigrella</i> sp.
<i>Monospilus dispar</i>	MISCELLANEOUS GROUPS
<i>Diaphanosoma leuchtenbergianum</i>	<i>Rhithropanopeus harrisi</i> (zoea larvae)
	<i>Balanus</i> sp. (nauplii)
	<i>Palaemon macrodactylus</i> (larvae)

crustaceans than mysids 7 mm long. Juvenile mysids, *i.e.*, ≤ 3 mm long, did not appear to consume crustacean prey.

Laboratory feeding experiments indicate that as copepod density increases, mysid predation also increases (Fig. 5). At low densities, almost no copepods were ingested, whereas at concentrations of 32/300 ml, almost half the copepods were eaten in 12 hr. Results of the field analysis are quite variable but indicate generally increased predation with increasing copepod density.

Feeding observations suggest that *N. mercedis* is not a particularly active predator. Mysids position themselves horizontally near the bottom or along the walls of the feeding chambers. Copepods were captured when drawn by feeding currents toward the first pair of thoracic appendages. Copepods were not captured until positioned ventral to the eyestalks, after which the mysid seized and held the copepod with its thoracic endopods while forming a cage-like structure with the remaining thoracic appendages. The prey was positioned below the mouthparts and consumed in its entirety, sometimes anterior first, sometimes posterior first. Copepods were often able to escape from the feeding current before becoming vulnerable. Ingested copepods appear light to dark brown in the guts of live mysids.

Neomysis mercedis appears to feed continuously, with a peak in activity for large mysids during darkness (Fig. 6). The number of copepods consumed per mysid was greater, and the percentage of unrecognizable material less, in larger mysids (≥ 11 mm) collected near midnight than in those collected during daylight. This pattern was not apparent in small mysids. Fine filter feeding appears to be a continuous process, since the number of diatoms per mysid did not vary significantly.

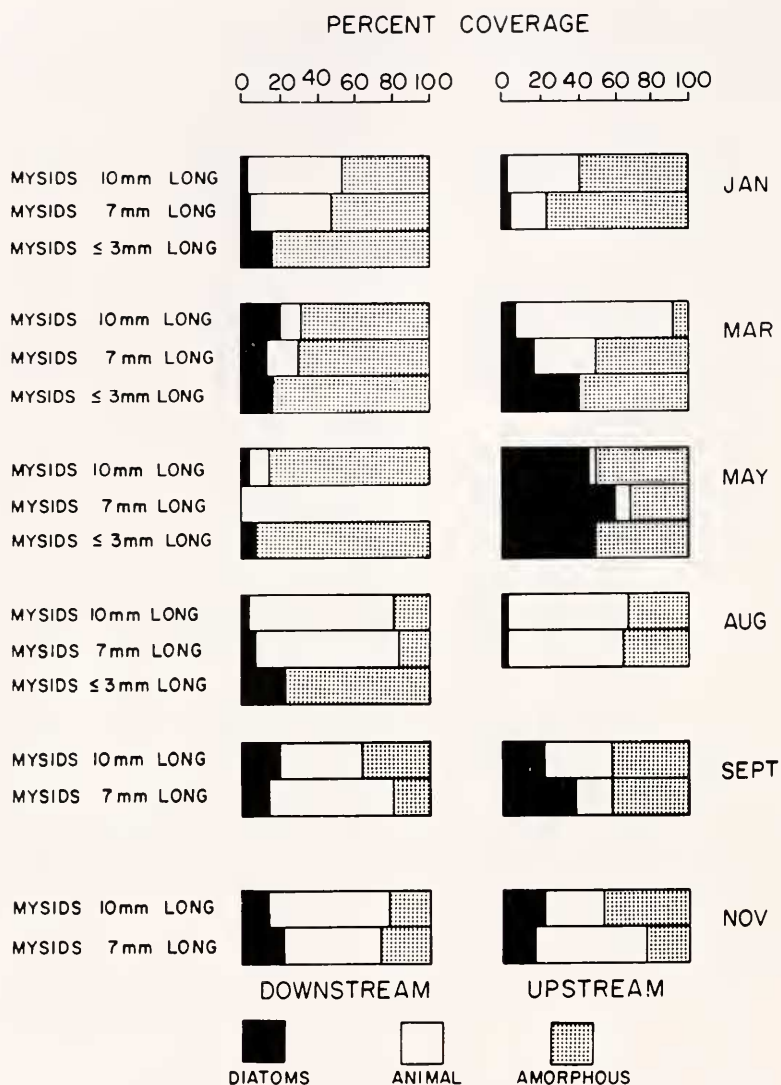


FIGURE 4. Percentage of gut-content filter-pad coverage attributable to phytoplankton, animal material, and amorphous materials, January–November, 1976.

DISCUSSION

Kost and Knight (1975) classified the amorphous material that was the most abundant material in the mysid guts as detritus. Detritus derived from vascular plants and inorganic particulate matter was rarely encountered in the present or previous study. The unidentifiable material present in the mysid guts may be the contents of fragmented algae or crustacean body fluids. Rybock (1978) found considerable "detritus" in the guts of specimens of *Mysis relicta* collected from areas of Lake Tahoe where no "detritus" existed and concluded that this material

was well digested and macerated prey. The role of detritus in the nutrition of *Neomysis mercedis* requires further study.

The selectivity patterns of mysids ingesting phytoplankton represent capturability based on size rather than true preference. *Melosira* and *Coscinodiscus*, the most frequently ingested phytoplankters, represent two of the largest algae available, with *Coscinodiscus* occurring as single cells that often exceed 50 μm in diameter and *Melosira* occurring as filaments of relatively large cells. *Skeletonema* occurred

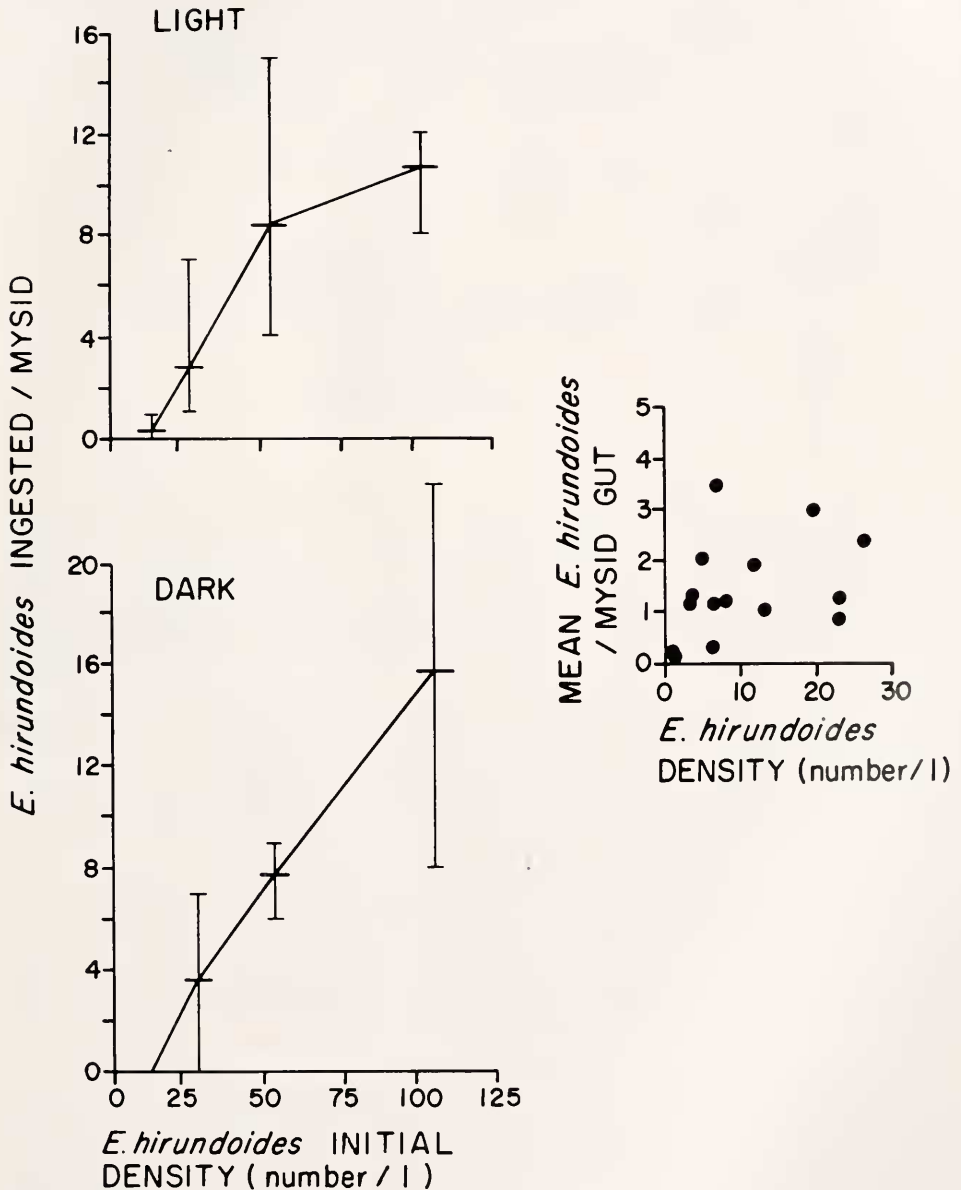
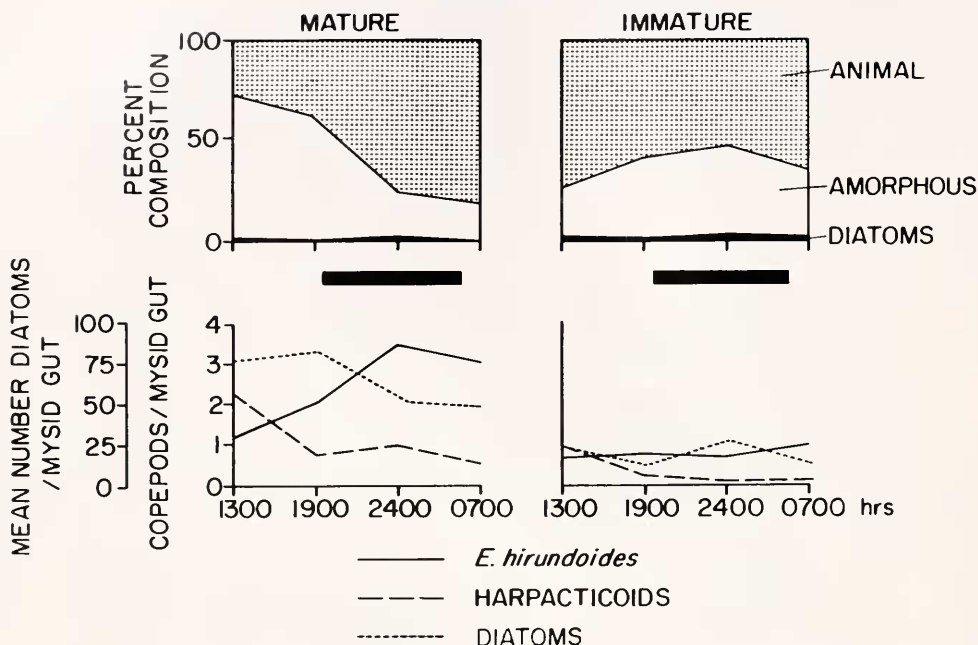


FIGURE 5. Number of specimens of *Eurytemora* ingested by *N. mercedis* in relation to *Eurytemora* density.

N. mercedis GUT CONTENTSFIGURE 6. Diel variation in *N. mercedis* gut contents, June 28, 1976.

in short filaments of small cells, generally less than 10 μm long, and in spite of its dominance in the phytoplankton was relatively unimportant in the mysid diet. *Merismopedia*, a small alga, generally occurring in a tetrad less than 5 μm wide, was not identified in the diet of *N. mercedis* although it was very abundant in the fall. Smaller mysids tended to feed on the smaller diatoms as well as the larger forms.

Similar results were reported for mature *M. relicta* from Lake Michigan (Bowers and Grossnickle, 1978). *M. relicta* was found to feed almost exclusively on the largest algal size fraction available, i.e., filamentous diatoms. Algae that passed through a 53- μm mesh were not consumed during *M. relicta* feeding trials. Grazing pressure by mysids on large filamentous diatoms may influence phytoplankton community composition, particularly in the spring.

Peak phytoplankton concentrations were significantly lower in 1976 than in any previous year since records were initiated, i.e., 1966 (Arthur and Ball, 1978). The low phytoplankton concentrations, believed to be due to the upstream movement of the entrainment zone (Arthur and Ball, 1978), may have been indirectly responsible for the poor success of the mysid population in 1976 (J. Orsi and C. Knutson, Calif. Dept. Fish and Game, unpublished).

The negative selection for copepod nauplii evident in the present study was also evident in Rybock's (1978) study of *M. relicta* in Lake Tahoe. Nauplii are apparently better able to avoid the mysids' feeding currents than are later copepod life stages.

Differences in feeding by various life stages of *N. mercedis* allow efficient partitioning of food resources, thus reducing intraspecific competition. Larger mysids

TABLE III

Caloric value of zooplankton and diatoms in guts of specimens of *N. mercedis*, from the San Francisco Bay-Delta Estuary, 22 January-16 November, 1976.

Upstream (Station M1)				
Date	11 mm mysids		7 mm mysids	
	Zooplankton cal/mysid $\times 10^{-2}$	Phytoplankton cal/mysid $\times 10^{-5}$	Zooplankton cal/mysid $\times 10^{-2}$	Phytoplankton cal/mysid $\times 10^{-2}$
22 Jan	1.1	1.1	0.3	0.7
26 Mar	4.1	1.0	3.3	0.7
26 May	0.6	24.0	0.2	1.2
28 Jun	3.0	1.6	1.3	1.7
02 Aug	1.5	1.0	1.2	1.5
21 Sept	1.6	*	0.7	*
16 Nov	3.0	*	0.7	*

Downstream (Station M7)				
22 Jan	1.0	0.6	0.5	0.8
26 Mar	1.9	0.4	0.4	0.2
26 May	1.2	24.0	0.3	0.4
28 Jun	—	—	—	—
02 Aug	1.9	0.7	0.5	0.4
21 Sept	0.7	*	0.5	*
16 Nov	2.3	*	0.2	*

* Cells fragmented, no estimates of total number of caloric equivalents made.

optimize net energy per unit feeding time by "selecting" the largest prey available. Juvenile mysids have a smaller range of prey available.

One of the most interesting aspects of feeding by omnivores is the relative contribution of various trophic levels to nutrition. Mysids feed as herbivores when small, whereas carnivory increases in importance in larger mysids. Mean gut contents were converted to caloric equivalents by empirically determined conversion factors to assess the relative contribution of herbivory and carnivory to ingestion by *N. mercedis* (Table III).

Carnivory accounted for > 90% of the energy represented by food material present in the guts of mysids ≥ 7 mm (Table III). Mysids would be expected to pass different foods through their guts at different rates and may assimilate them with different efficiencies (Pechén-Finenko and Pavlovskaya, 1973). That could alter the above estimates (Table III) but should not change the overall patterns. The relative role of predation to the nutrition of *M. relicta* in Lake Tahoe is similar (Rybock, 1978).

Phytoplankton populations were very low in the Delta in 1976. That may have contributed to an increased importance of carnivory. However, conversion of gut-content information presented by Kost and Knight (1975) to caloric equivalents (assuming, conservatively, that copepods consumed = 1/10 of crustacean fragments detected) indicates that predation accounted for about 84% of the food energy values. Although herbivory may be of direct importance during blooms (Bowers

and Grossnickle, 1978), predation appears to be the most important feeding mode for *N. mercedis* in the Sacramento-San Joaquin Delta.

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SUMMARY

The diet of the opossum shrimp, *Neomysis mercedis*, in the Sacramento River Estuary was studied in relation to food availability, i.e., plankton, from January through November, 1976. The composition of the diet of *N. mercedis* varied in relation to mysid size and prey availability. Mysids exhibited strong positive selection for the large diatom prey species while "avoiding" small diatom prey. Although diatoms were the most abundant prey identified from the guts of specimens of *N. mercedis* it was determined that predation on rotifers and copepods accounted for > 80% of the energy consumed by other-than-juvenile mysids (≥ 7 mm in length). Juvenile mysids (≤ 3 mm in length) ingested rotifers when rotifers were abundant but were not found to consume copepods. Laboratory feeding experiments indicate a density-dependent feeding by *N. mercedis* on copepods, i.e., as copepod density increases mysid predation on copepods also increases. Feeding observations indicate that *N. mercedis* is not a particularly active predator, capturing prey drawn into its feeding current but not actively pursuing prey. *N. mercedis* appears to feed continuously, with a peak in activity for mature mysids during darkness, a pattern not apparent in immature mysids. Consumption of the detritus was not considered significant. Although herbivory may be of direct importance during the spring diatom increase, carnivory was the major source of energy for *N. mercedis* in the Sacramento River during 1976.

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